

NEW VICTORELLIDS (BRYOZOA, CTENOSTOMATA) FROM NORTH AMERICA: THE USE OF PARALLEL CULTURES IN BRYOZOAN TAXONOMY

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ABSTRACT

Three species of the Victorellidae (Bryozoa, Ctenostomata) were found in North America and were cultivated in Braunschweig (W. Germany). Two are new species, *Victorella pseudoarachnidia* sp. nov. and *Tanganella appendiculata* sp. nov. *Bulbella abscondita* Braem is reported for the first time from Massachusetts (U. S. A.). Identification of victorellids requires the examination of living animals. The species considered here were identified by observation of live material collected in North America and Germany and of living individuals cultured from that material.

INTRODUCTION

Kent (1870) described a species of the bryozoa (class Gymnolaemata, order Ctenostomata) as *Victorella pavid*a, based on material collected in brackish waters in England. Kraepelin (1887) concluded that some specimens interpreted primarily as immature *V. pavid*a (from the Ryck River, Germany) represented a new species and named it *Paludicella mülleri*. Braem's (1911) first opinion was that *P. mülleri* was only a developmental stage of *V. pavid*a.

After many years of observation of living victorellids from northern Germany, Braem (1951) split the literature species *Victorella pavid*a into three species. After a comparison with preserved *V. pavid*a from England, Braem designated certain specimens to be *V. pavid*a, characterized by the seasonal production of an intertentacular tube, the absence of brooded embryos, and the location of the cardiac sphincter far above the central stomach. Victorellids which produced no intertentacular tube, brooded embryos internally, and possessed a cardiac sphincter near the central stomach were placed into a new genus as *Tanganella mülleri*. Specimens characterized by shorter peristomial tubes, a small intertentacular tube, external brooding of embryos, and the cardiac sphincter moderately above the central stomach were assigned to a new genus and new species, *Bulbella abscondita*.

Although these distinguishing characteristics were adequately described by Braem (1951), Brattström (1954) expressed some doubt about Braem's splitting of *V. pavid*a. Brattström apparently overlooked the important fact that, unlike Braem, most workers described new species from preserved specimens. Preserved ctenostomes, however, do not usually exhibit all features necessary for identification. The characteristics described by Braem (1951) have been confirmed on living specimens from other localities (Jebam, 1969, 1976). These studies on living victorellids, then, suggest that many specimens identified from preserved material may have been other species.

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Another facet of the taxonomic problem in the Victorellidae is evident in several North American reports. Osburn (1944) studied *Victorella pavida* from the Chesapeake Bay (Atlantic Coast, U. S. A.) and reported that the colonies collected from the upper (less saline) end of the bay tended to be less branched. However, his photograph (1944, Pl. V) of *V. pavida* shows brooded embryos and therefore suggests, according to Braem's (1951) work, that at least a part of Osburn's material was not *Victorella*.

Rogick (1949) described *Nolella blakei* from Woods Hole, Massachusetts (Atlantic Coast, U. S. A.) and compared it to other ctenostomes. Soule (1957) identified specimens from the Salton Sea (California, U. S. A.) as *N. blakei* and *V. pavida*. He incorrectly synonymized *Tanganella mülleri* with *V. pavida*, but did not discuss the major distinguishing characteristics used by Braem (1951). Rogick (Soule, 1957) confirmed Soule's identification of the preserved material. Examination of Soule's Salton Sea specimens revealed victorellids but no *Nolella* (Jebam, personal observations, 1977).

Hyman (1959) was one of the few zoologists who acknowledged Braem's (1951) results, but she misinterpreted his comments on a crucial point. She (1959, p. 333) wrote that "brooding arrangements vary greatly, even within the same genus . . .", and she misquoted Braem in her statement that in *V. pavida* "each egg as it emerges from the supraneural pore is caught in a depression of the adjacent dorsal body wall, and eventually passes into the coelom of the dorsal side of the vestibule where three or four developing embryos may be found." These comments and her figures 125C and 125D apply not to *V. pavida* but to *T. mülleri*. *Victorella pavida* produces an intertentacular tube (not a simple pore) and does not brood embryos (Braem, 1951; Jebam, 1969, 1976).

Subsequent investigators essentially ignored Braem's (1951) findings and continued to use predominantly external characteristics for the identification of the victorellids (Prenant and Bobin, 1956; Sacchi and Carrada, 1962; Carrada and Sacchi, 1964; Everitt, 1975; Poirrier and Mulino, 1977). Osburn (1944) and Soule (1957) synonymized various forms with *V. pavida*. Osburn (1944) and Everitt (1975) independently suggested that branching, the formation of adventitious zooids (another external characteristic), correlates positively with salinity. Poirrier and Mulino (1977) confirmed this correlation in 49 of 52 samples but suggested that "other factors . . . may also influence branching."

The confusion evident in taxonomic and ecological papers on *Victorella pavida*, the relatively poor condition of *V. pavida* specimens in the British Museum (Jebam, Everitt, personal observations, 1980), and the apparent lack of any specimens of *Nolella blakei*, including Rogick's material from Woods Hole (Everitt), led to the current investigation. During the fourth conference of the International Bryozoological Association in Woods Hole, Massachusetts (U. S. A.) in September of 1977, we discussed some problems in victorellid taxonomy. The purposes of this investigation were to collect *N. blakei* from the type locality, to collect victorellids from the Salton Sea (California, U. S. A.), to culture any victorellids collected, and to revise the taxonomy of these North American victorellids on the basis of observations of living animals.

MATERIALS AND METHODS

In September of 1977 and in August of 1978, victorellids were collected from the bridge pilings at the outlet of Lagoon Pond on Martha's Vineyard Island (Mass., U. S. A.), the type locality for *Nolella blakei*. Living colonies were observed and

were either preserved in 10% formalin or cultured in the laboratory (Braunschweig, W. Germany). In October of 1977, victorellids were collected in the Salton Sea (California, U. S. A.) and were treated likewise.

The methods for culturing bryozoans were described previously (Jebam, 1977a, 1977b, 1979). The methods for culturing victorellids were developed anew according to earlier results with other bryozoan species (Jebam, 1980b). For comparative morphology the victorellids were maintained at 21–23°C and 14–16‰ salinity and were fed the food mixture J5b, the composition of which was determined experimentally. The descriptions of the species provided here are based on specimens cultivated under these conditions (Jebam, 1980b). Details on morphology and techniques are given under "Experimental Biology".

After the animals attained sexual maturity, they were compared with living victorellids collected in Germany and with earlier descriptions based on living specimens. Cultures of *Victorella pavida*, *Tanganella mülleri*, and *Bulbella abscondita* have been maintained in the laboratory of the senior author (*T. mülleri* since 1968). Colonies subcultured from the holotype specimens of the American victorellids discussed here are being maintained for further study; Louisiana (U. S. A.) specimens are also being cultured in Braunschweig.

Drawings of the species described here were prepared by Jebam from photographs of living animals. Paratype specimens are in the collections of the authors.

SYSTEMATIC TREATMENT AND RESULTS

Victorella pseudoarachnidia sp. nov.

Holotype material: Collection of D. Jebam, 1978-10-10-1.

Paratype material: U. S. National Museum of Natural History, Smithsonian Institution (Washington, D. C.), Cat. No. 36, USNM No. 292472; Bryozoan Collections of the Allen Hancock Foundation, Univ. of Southern California at Los Angeles, No. 185.1; British Museum (Natural History), London; personal collections of authors.

Name: The cystid appendages suggest superficial similarities to an arachnidioid form.

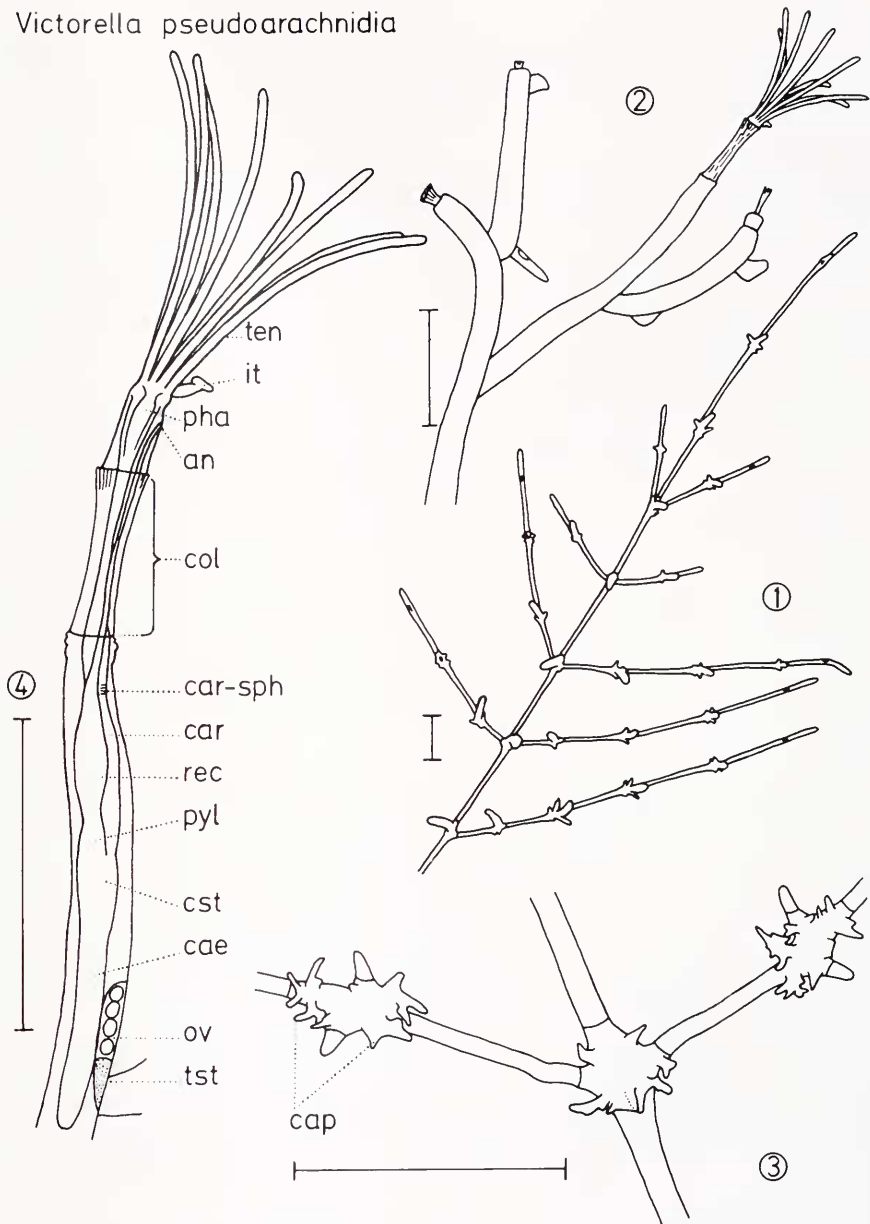
Synonyms: "*Victorella pavida* Kent" and "*Nolella blakei* Rogick" *sensu* Soule, 1957 (nec. *Victorella pavida* Kent, 1870, *sensu* Braem, 1951; nec *Nolella blakei* Rogick, 1949).

Type locality: Salton Sea, California, U. S. A.

Description: The colonies of *Victorella pseudoarachnidia* are composed of serially arranged zooids (Fig. 1). Each zooid usually produces one distal and two lateral daughter zooids at the sides of the basal part of the cystid. The branching pattern of these daughter zooids is regular and symmetrical. Older zooids can produce adventive zooids by forming "high buds" ("Hochknospen") on the anal or lateral sides of the peristomial tube (Fig. 2). In addition to the encrusting colony parts ("*forma encrustans*" *sensu* Braem, 1951) are often free, non-encrusting branches ("*forma ascendens*" *sensu* Braem, 1951) of zooid series formed at the borders of the substrate pieces or originating from the high buds. The colony in this species thus has a habit somewhat similar to that of most other victorellids.

Each zooid is composed externally of two main parts, a basal proximal part (usually encrusting the substrate) and an upright peristomial tube. The basal part is broad at its distal end and narrow proximally; the proximal narrowing usually is relatively abrupt.

Encrusting zooids of *V. pseudoarachnidia* have cystid appendages which usually originate on each side of the budding sites of the daughter zooids. The basic pattern

Victorella pseudoarachnidia

FIGURES 1-4: *Victorella pseudoarachnidia* sp. nov. (1) part of the holotype colony demonstrating the budding pattern in an encrusting colony; (2) "high buds" and adventive zooids in lateral view; (3) three zooids in basal view demonstrating the budding pattern and the cystid appendages; (4) sexually mature zooid in lateral view; an, anus; cae, caecum; cap, cystid appendages; car, cardia; car-sph, cardiac sphincter; col, collar; cst, central stomach; it, intertentacular tube; ov, ovary; pha, pharynx; pyl, pylorus; rec, rectum; ten, tentacles; tst, testis; scale bars represent 1 mm.

consists of 9-10 sites for the potential formation of cystid appendages (Figs. 3, 11). All cystid appendages may branch weakly into two to several tips. One or a few of the distinct appendages may be vestigial or absent. The branching of the ap-

pendages may occur under the central basal part of the cystid so that only the tips project visibly beyond the lateral margin of the cystids. The non-encrusting zooids form no (or vestigial) cystid appendages. The formation of cystid appendages is generally variable and somewhat modifiable but never occurs on the narrow, most proximal part of the basal cystid. The origin of all the tips of the cystid appendages from restricted and rather distinct sites of a zooid can often be detected only if the animals are growing on glass slides and are illuminated sufficiently. Otherwise the shape of the central basal cystid parts may superficially resemble an arachnidoid form. In the victorellids, the appendages of different zooids may touch each other but never really fuse histologically as they can in typical arachnidoid forms.

The peristomial tubes grow stepwise upward by each case of polypide replacement and may thus attain a considerable length (to about 1 cm with polypide retracted). The diameter of the peristomial tube is about 220 μm .

The autozooids of *Victorella pseudoarachnidia* always have 8 tentacles. Sexually mature zooids have a trumpet-shaped intertentacular tube with a widely flared opening, through which the ova are released (Fig. 4). This species does not brood embryos, either in the neck region or in the tentacle sheath. Freshly released ova are spindle-shaped and whitish and become globular after approximately fifteen minutes.

The gut anatomy of this species shares two essential attributes with that of *Victorella pavidia*: location of the cardiac sphincter considerably above the central stomach (Fig. 4) and absence of a gizzard.

Victorella pseudoarachnidia produces lasting buds which may have irregularly shaped marginal appendages and which, in older stages, have a greyish or dark brown to almost black cuticle. The storage products in the ova and in the lasting buds are whitish.

The accompanying fauna in the type locality of *V. pseudoarachnidia* included the stolonate ctenostome *Bowerbankia cf. gracilis* Leidy and the kamptozoan (entoproct) *Barentsia benedeni* (Foettinger) (Jebam, field observations, 1977). Soule (1957) did not report these species from his Salton Sea samples.

Differentiating characteristics of similar forms: (1) In other species of *Victorella* described so far, there has been no mention of the formation of such types of branched cystid appendages at restricted sites of the zooids. (2) Species of *Tanganella* differ in the location of the cardiac sphincter near the central stomach, the formation of an intertentacular pore, the brooding of embryos, and the form and arrangement of the cystid appendages. (3) Almost all species of the superfamily Arachnidioidea have the potential to produce cystid appendages, but these appendages are usually narrow and rarely branched and may originate also from the narrow proximal part of the cystid. In the Arachnidioidea the appendages and branches may actually fuse histologically and may produce new zooids at the fusion sites (Fig. 11).

Tanganella appendiculata sp. nov.

Holotype material: Collection of D. Jebam, 1978-10-10-2.

Paratype material: U. S. National Museum of Natural History, Smithsonian Institution (Washington, D. C.), Cat. No. 36, USNM No. 292473; Bryozoan Collection of the Allan Hancock Foundation, Univ. of Southern California at Los Angeles, No. 186.1; British Museum (Natural History), London; personal collections of authors.

Name: The cystids usually have appendages at restricted sites.

Synonyms: part of the material of *Victorella pavida sensu* Osburn (1944), according to his description (nec. *Victorella pavida* Kent, 1870, *sensu* Braem, 1951).

Type locality: Lagoon Pond, Martha's Vineyard Island, Massachusetts, U. S. A.

Description: The colony of *Tanganella appendiculata* is composed of serially arranged zooids (Fig. 5). Each zooid usually produces one distal and two lateral daughter zooids on the sides of the basal part of the cystid. Older zooids can form adventive zooids by producing "high buds" on the anal and lateral sides of the peristomial tube (Fig. 6). In addition to the encrusting colony parts (forma encrustans) free, nonencrusting branches of zooid series often may be formed at the borders of substrate pieces or may originate from "high buds" (forma ascendens). The colony form of this species thus resembles that of most other victorellids.

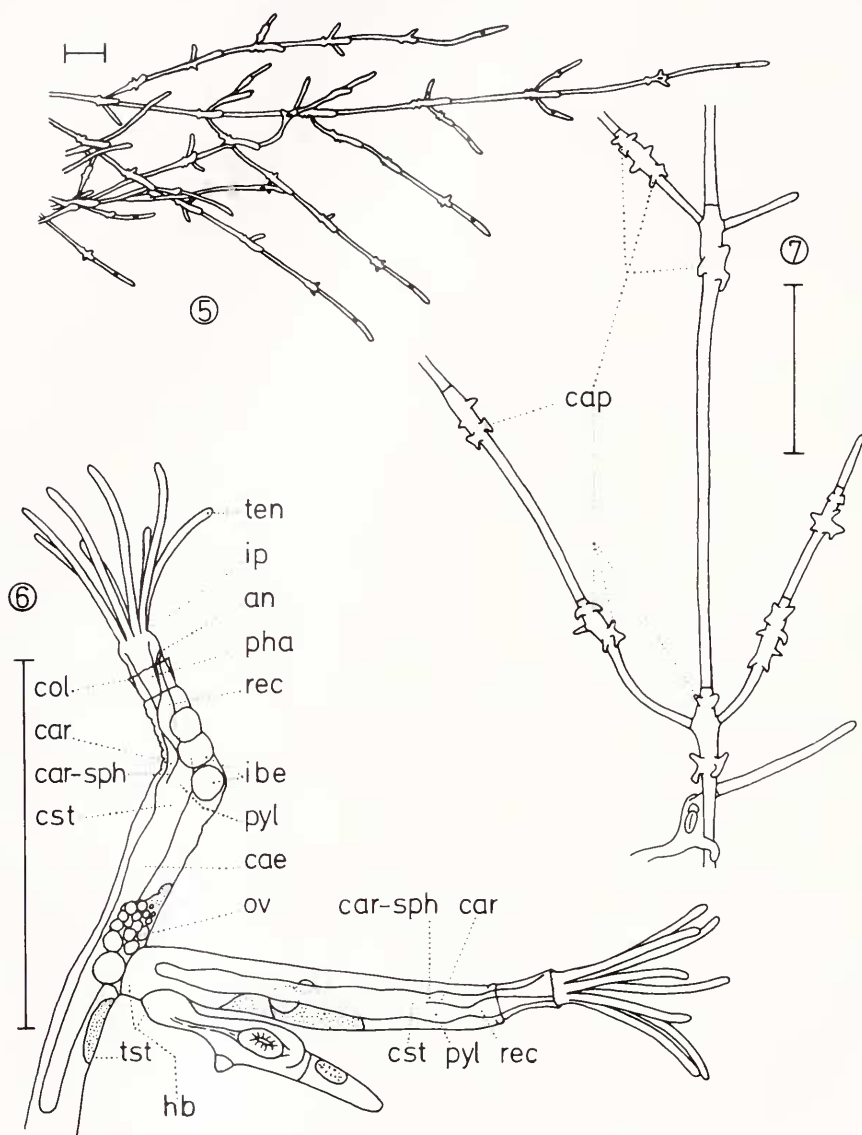
The zooids are composed externally of two main parts, a basal proximal part (usually encrusting the substrate) and an upright peristomial tube. The basal part is somewhat broadened at its distal part and gradually narrows proximally.

Encrusting zooids of *Tanganella appendiculata* usually have typical cystid appendages. One or two emerge, usually latero-proximally on each side, at the sites from which the lateral daughter zooids originate from the basal part of the cystid. One or two other pairs of cystid appendages may be formed anterior to the budding places of the side-branches (Fig. 7). However, the cystid appendages, especially the distal pair, are sometimes vestigial or absent. The appendages may be so minute that they are detectable only if the zooids are growing on glass slides and are adequately illuminated. These appendages, of course, can be overlooked easily in specimens from the natural habitat, especially if they are encrusting a rugged substrate. The cystid appendages sometimes branch into several tips and even into four separate appendages. In this species, the cystid appendages always originate from the sides of the distal, broader portion of the encrusting part of the cystid, never from the narrow, proximal portion. Non-encrusting zooids produce no cystid appendages (or only vestigial ones). The appendages from different zooids may touch each other but never fuse histologically.

The younger peristomial tubes are always considerably inclined distally; older ones may become raised almost perpendicular to the basal part of the cystid. The peristomial tubes grow upward in steps by each case of polypide replacement in the same cystid and may attain a length of approximately 9 mm (polypide retracted). The diameter of the peristomial tube averages 160 μm .

The autozooids of *Tanganella appendiculata* always have 8 tentacles. Sexually mature zooids have an intertentacular pore through which the ova are released. This very narrow pore is discernible in living animals only during the release of the egg through the pore.

The ova are apparently fertilized during their passage through the intertentacular pore. At that time they are dumbbell-shaped or irregularly shaped but not spindle-shaped. The released ova are pressed to the anal neck region, where they adhere to the body wall. Later they are invaginated into a pocket of the body wall; the embryos remain there until they develop into larvae (Fig. 6). Up to six embryos may be brooded in the median line of the anal neck region of one zooid. The polypide apparently remains active throughout the period of ova release (several days) but later may be resorbed. The larvae slip through the breaking body wall into the water and may swim for several hours or days (even more than 10 days!) until they find an acceptable place for settlement. The first polypide of the ancestor of *Tanganella appendiculata* has 6 tentacles.

Tanganella appendiculata

FIGURES 5-7: *Tanganella appendiculata* sp. nov. (5) part of the holotype colony demonstrating the budding pattern in an encrusting colony; (6) sexually mature zooid with adventive zooid and "high buds," hb, in lateral view; (7) some zooids in basal view demonstrating the budding pattern and the cystid appendages; ibe, internally brooded embryos; ip, site of the intertentacular porus; for other abbreviations see Figs. 1-4; scale bars represent 1 mm.

Lasting buds are usually formed in larger colonies. The cuticle of older lasting buds becomes light brown by thickening. The reserves of the lasting buds, the ova, and the embryos are white.

The anatomy of the gut of *Tanganella appendiculata* is similar to that of *T. mülleri*. The cardiac sphincter is very close to the central stomach, a characteristic given by Braem (1951) for the genus. No gizzard is formed. The caecum is considerably longer and more slender than in *Victorella* in proportion to the size of the polypide.

The accompanying fauna in the type locality included *Bowerbankia gracilis* Leidy, *Barentsia benedeni* (Foettinger), and *Bulbella abscondita* (see below).

Differentiating characteristics of similar forms: (1) *Tanganella mülleri* (Kraepelin) *sensu* Braem (1951) forms 7 tentacles in the first polypide generation of the ancestrula. Braem (1951), who made most of his observations of colonies growing on natural (non-glass) substrates, did not describe cystid appendages in *T. mülleri*. These structures have now been detected under culture conditions for both species. Under certain salinity ranges and dietary conditions, *T. mülleri* may form comparatively smaller cystid appendages at 5 sites of a cystid, 2 latero-proximally and 3 distally from the budding sites of the side branches (Fig. 11). The appendages, however, especially the distal ones, are often absent or vestigial. In the main branches, the encrusting basal cystid parts are at least 30% shorter in *T. mülleri* than in *T. appendiculata* (under the same growth conditions), but this length may vary greatly in both species with external conditions. As Braem (1951) explained, contrary to the assumptions of various other authors, "*Paludicella mülleri*" respectively *Victorella pavida* forma *mülleri* in the sense of Ulrich (1926) is not *Tanganella mülleri* but *Bulbella abscondita*. Nevertheless, Prenant and Bobin (1956) ignored Braem's (1951) correction and erroneously maintained the incorrect identification and synonymy of Ulrich (1926). (2) *Victorella pseudoarachnidia* differs from *Tanganella appendiculata* in the location of the cardiac sphincter farther above the central stomach, in the formation of an intertentacular tube, in not brooding embryos, and in the form and arrangement of cystid appendages. (3) The species of the superfamily Arachnidoidea show the same differences as with *Victorella pseudoarachnidia* (Victorelloidea).

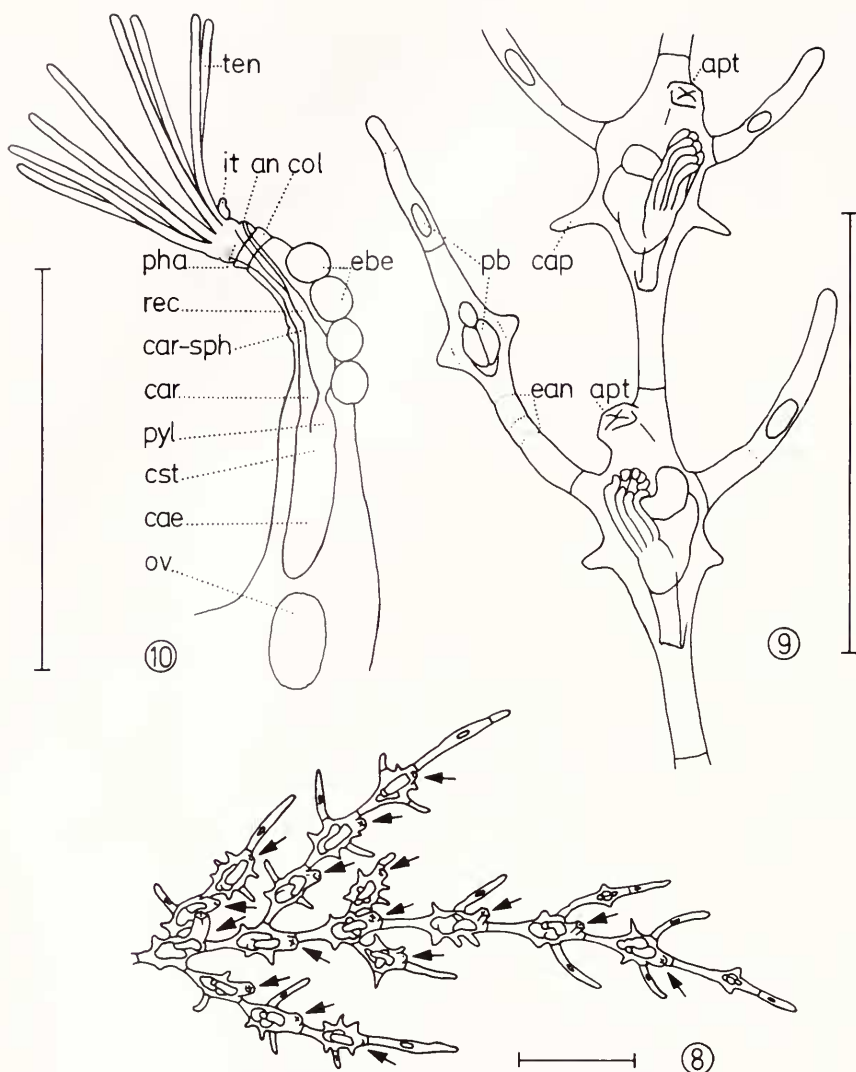
Bulbella abscondita

Paratype material: U. S. National Museum of Natural History, Smithsonian Institution (Washington, D. C.), Cat. No. 36, USNM No. 292474; Bryozoan Collection of the Allan Hancock Foundation, Univ. of Southern California at Los Angeles, No. 187.1; British Museum (Natural History), London; personal collection of authors.

Locality: Lagoon Pond, Martha's Vineyard Island, Massachusetts, U. S. A.

Description: In most features the specimens found in this study resemble those described by Braem (1951). The colony is composed of serially arranged zooids (Fig. 8). Each zooid usually produces one distal and two lateral daughter zooids. Adventive zooids originating from high-buds occur rarely on older zooids. In old colonies, the zooids are crowded and grow irregularly. In addition to the encrusting zooids, the colony rarely may produce free, non-encrusting branches. The latter zooids occur mainly at the borders of the substrate but also may arise from the flat areas; their production is related partly to the diet.

The young zooids are comprised almost entirely of the basal cystid part, which is broader distally and slender proximally (Fig. 9). Although the polypide bud starts to develop as a median epidermal invagination (the usual process in ctenostomes), the aperture of the young encrusting zooids is always lateral. Within one



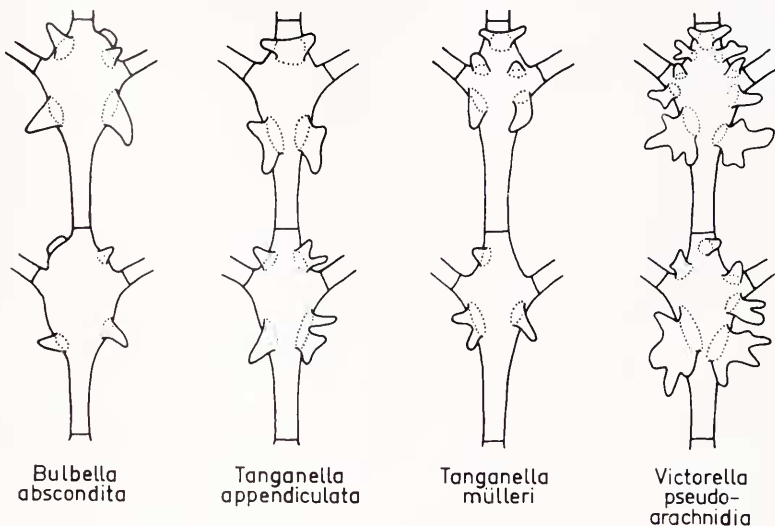
Bulbella abscondita

FIGURES 8-10: *Bulbella abscondita* (8) and (9) parts of the holotype colony demonstrating the budding pattern in an encrusting colony (arrows indicate the asymmetrical position of the apertural papillae); (10) sexually mature zooid in lateral view; apt, apertural papillae; ean, external annulations caused by too strong brushing; ebe, externally brooded embryos; pb, polypide buds; for other abbreviations see Figs. 1-4; scale bars represent 1 mm.

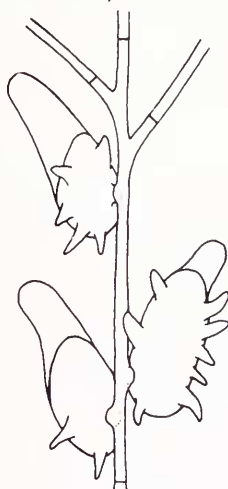
distally arranged zooid series, the right or left position of the initial apertures may vacillate irregularly, a kind of enantiomorphic effect. Only a small apertural papilla is formed in young zooids primarily with the first polypide generation. The replacement of the polypides in the same cystid causes a modest elongation of the peristomial tube, which becomes shifted to the median line in older, crowded zooids.

SCHEMATICAL SYNOPSIS OF TYPES OF CYSTID APPENDAGES

SERIALLY ARRANGED FORMS: VICTORELLOIDS (IN BASAL VIEW):



STOLONATE FORM, VESICULARIROID:

*Buskia nitens*

ARACHNIDIROID FORM:

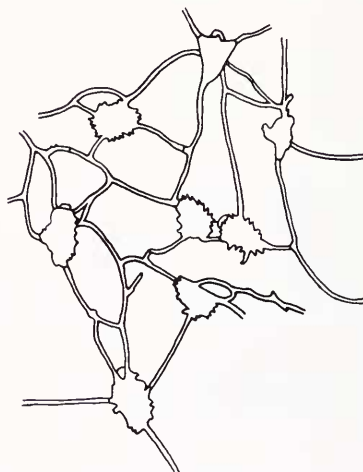
*Nolella blakei*

FIGURE 11: Schematical synopsis of types of cystid appendages (in basal view). In the victorellid species, the upper zooid demonstrates the ground plan of the arrangement of the appendages, while the lower zooid shows an example of a more or less common arrangement. The sketch of *Buskia nitens* is an abstraction from various observations and published figures. The sketch of *Nolella blakei* is redrawn from Rogick (1949, fig. 5) but reversed in an assumed basal view. (All examples are drawn at different scales.)

The peristomial tubes may attain a length of approximately 3–4 mm and a diameter of approximately 260 μm .

Encrusting zooids of *Bulbella abscondita* often form cystid appendages on the sides of the broader, distal part of the basal region of the cystid but never on the

narrower proximal part. Of four potential sites from which an appendage may emerge, 0–4 may actually produce one (Figs. 8, 9, 11); the number produced depends partly on diet conditions. These distinct sites for the cystid appendages are proximal and distal to the budding sites of the side-branches. The cystid appendages of different zooids may touch each other but do not fuse histologically.

The autozooids of *Bulbella abscondita* have 8 tentacles. Sexually mature zooids have an intertentacular tube with a narrow outlet through which the ova are released (Fig. 10). The ova are affixed to the ano-median line (sometimes to the ano-lateral side) on the polypide neck region. There the embryos (up to 6 per zooid) become larvae but are not invaginated into pockets of the body wall. The polypide of the mature zooid remains active during the ova-releasing period. The color of the reserves in the ova, the embryos, and the young larvae varies with diet and ranges from light yellow to almost white. The developed larvae are released and may swim for a few hours or days until they settle. The first polypide generation of the ancestrula has 7 tentacles (as in the typical form, Braem, 1951).

Some dormant buds, which were hidden under older zooids and were growing on glass slides, contained very light yellowish yolk and small polypide buds. The dormant buds found in this strain, however, have usually and essentially the shape of incompletely developed zooids but rarely of typical lasting buds found in other ctenostomes.

Braem (1951) stated that *Bulbella abscondita* usually has a gizzard with teeth but that the dentation may range from fully developed dentation to complete absence of teeth. In the North American specimens, a muscular proventriculus is present, but a true gizzard has not yet been observed. The cardiac sphincter is far above the central stomach and is more easily discernible in living animals during typical peristaltic movements of the gut. The caecum is comparatively short and stout. (For further details see Braem, 1951.)

Although there are some physiological differences between the North American strain and the Ryck (Germany) strain, the distinction is not yet sufficient to establish a separate species. We do not know whether the North American form can penetrate rotten wood as can the European form. The German form of *Bulbella* is being parallel-cultured in the laboratory at Braunschweig.

Differentiating characteristics of similar forms: (1) The species of the superfamily Arachnidoidea have the same differences as with *Victorella pseudoarachnidia*. (2) *Buskia nitens* has true stolons limited by septa. This species also prefers higher salinity (down to polyhaline) but never tolerates oligohaline conditions as does *Bulbella*.

EXPERIMENTAL BIOLOGY

The discrimination of species in the Victorellidae requires living and sexually mature animals (Braem, 1951; Jebram, 1969, 1976). Two main factors controlling growth and attainment of sexual maturity in brackish-water bryozoans are nutrition and temperature (Jebram, 1973a, 1975). In North American victorellids discussed here, these factors, especially food, were investigated by various qualitative tests.

Based on prior studies of brackish-water bryozoans (Jebram, 1975, 1977b), diet composition for the new bryozoan strains was established by experience (Jebram, 1980b). The food mixture J5b (Jebram, 1980b) was prepared especially for the cultivation of *Bulbella abscondita* but is suitable also for other bryozoans. *Bulbella* becomes sexually mature with this diet. Under laboratory conditions, ova and embryos seemed to attain the typical light yellow color only by addition of those food

species containing considerable amounts of carotenoids, *e.g.*, haptophyceans, chrysophyceans, bacillariophyceans. Some of the light yellow larvae produced with this diet metamorphosed successfully to ancestrulae and initiated the formation of a new colony generation. A diet mixture containing too much *Cryptomonas* species caused an earlier shifting of the apertural papilla from the cystid side toward the median line and an earlier and more pronounced elongation into a peristomial tube. The latter finding agrees with the observations made on *Bowerbankia* species and *Buskia nitens* (Jebram, 1973a, 1973b).

Although *Tanganella mülleri*, *T. appendiculata*, and *Victorella pseudoarachnidia* thrived and matured sexually with the food mix J5b, these species grew much better with a diet including *Oxyrrhis marina* (food mix J5h). This phagotrophic dinoflagellate is a very good food also for many other bryozoan species (Jebram, 1969, 1975, 1980a,b). Surprisingly, *Oxyrrhis*, presumably due to its taste, is very sparingly accepted by *Bulbella abscondita*. Therefore, *Oxyrrhis* should not be fed to *Bulbella* but may well be used for other victorellids. Diets containing *O. marina*, however, require a renewal at least each second day because the phagotrophic species soon alters drastically the composition of the diet preparation. Additionally, overaged cultures of *Oxyrrhis* may have toxic effects on the bryozoans (Jebram, 1975). If *Oxyrrhis* is used as a mono-food for a prolonged period, unusual growth forms may result. Further details concerning general problems of the nutrition of bryozoans have been discussed earlier (Jebram, 1977a,b, 1979, 1980a,b).

Even under the same external conditions (*e.g.*, food, salinity, temperature), all four victorellids cultivated in the Braunschweig laboratory (*Victorella pseudoarachnidia*, *Tanganella appendiculata*, *T. mülleri*, *Bulbella abscondita*) had different growth rates and formed different colony habits (qualitative observations). Although the different colony habits can be observed easily when the specimens are side by side, these differences can be described less easily. This difficulty was perhaps one of the reasons for the confusion in the taxonomy of this group of bryozoans in the past. *Victorella pseudoarachnidia* exhibited the fastest growth rate and formed larger bushes of the forma ascendens. The zoaria of *Tanganella appendiculata* colonized the substrate more quickly (by greater elongation of the narrow proximal cystid part) than those of *T. mülleri*, but the latter attained sexual maturity sooner. In *Victorella* and *Tanganella* the growth rate and the formation of adventive zooids by high buds were considerably greater, and sexual maturity occurred earlier with the food mixture J5h (with *O. marina*) than with J5b. *Bulbella abscondita* showed the slowest growth rate.

The formation of cystid appendages was apparently more or less influenced by unknown dietary components in all the victorellids cultivated. Additionally, in lower salinity ranges (5–8‰), *Tanganella mülleri* formed no (or only vestigial) appendages, but in *T. appendiculata* the appendages only became small (or were sometimes absent). With greater salinity (about 15‰) the formation of the appendages increased in both species of *Tanganella*. In *Victorella pseudoarachnidia*, however, the growth of cystid appendages seemed unaffected by variation of salinity within ecologically acceptable ranges.

Tanganella mülleri, *T. appendiculata*, and *Bulbella abscondita* inhabit areas in which the water temperature seldom reaches and rarely exceeds 20°C. Accordingly, these species attained sexual maturity in the laboratory at temperatures of 19°C or lower. On the other hand, the Salton Sea (California), from which *Victorella pseudoarachnidia* was collected, is in a warm semi-desert area (water temperature 26°C at 0900 on 9 Oct. 1977). Therefore this species must be adapted to higher temperature ranges. Accordingly, *V. pseudoarachnidia* seemed to require

a temperature above 20°C for sexual maturation in the laboratory but grew well asexually at lower temperatures.

DISCUSSION

Cystid appendages in ctenostome taxonomy

One reason for seeking ctenostomatous bryozoans in Lagoon Pond on Martha's Vineyard Island (Mass., U. S. A.) in September of 1977 was Rogick's (1949) report of *Nolella blakei*, which she thought lived in that pond. Although her specimens of *N. blakei* have not been found again, her description is undoubtedly that of an arachnidioid species. Instead of the expected species, we were surprised to find an obvious victorelloid, a species of *Tanganella*.

Rogick (1949) noted that she collected benthos from Lagoon Pond but that *Nolella blakei* was not seen initially in that material. She stored the material in watch glasses in large aquaria which were supplied with running sea water piped from the nearby bay. After nine days she discovered a ctenostome in those glasses and described *N. blakei*. It now appears that *N. blakei* does not inhabit the brackish Lagoon Pond but that it is a marine species (like most other species of *Nolella*) and that Rogick's colony originated from larvae in the seawater piped from the bay. Rogick did not mention any species of the Victorelloidea in her Lagoon Pond material.

The cystid appendages of *Tanganella appendiculata* were not observed in our first specimens from Lagoon Pond, in which they grew crowded with *Bowerbankia gracilis* on natural substrates. When the *Tanganella* material was cultured on glass slides in the laboratory at Braunschweig, the cystid appendages were detected. Another unexpected discovery was that the European *Tanganella mülleri* can also produce cystid appendages under certain conditions; Braem (1951) did not describe such appendages in *T. mülleri*.

These observations generated two basic questions. First, are there two separate species of serially arranged ctenostomes in the Salton Sea (California) as reported by Soule (1957)? The senior author examined Soule's specimens and, after additional studies on living animals, concluded that Soule's "*Nolella blakei*" is identical with his *Victorella* "*pavida*". Soule's specimens of "*Nolella*" were actually those zooids of *Victorella* which were growing on glass bottles. The cystid appendages on glass can be seen more easily than on other substrates and also can be removed more readily. Soule's *Victorella* "*pavida*" was mainly material from other types of substrate, and the cystid appendages were probably lost or damaged during removal of the zooids. One of Soule's drawings (1957, Fig. c) shows zooids of *V. "pavida"* with appendages, but the morphology of the appendages was not sufficiently analyzed. Such analysis requires proper procurement and preparation of specimens. The following features common to all known serially arranged ctenostomes from the Salton Sea indicate that they all belong to one species, a *Victorella*: constant number of tentacles (8); intertentacular tube; absence of brooding of embryos; anatomy of the gut; difference in arrangement and growth potential of cystid appendages as compared to arachnidioid species (see below).

The second basic question is whether the presence of cystid appendages in the true victorellids means that there are no principal differences between the Victorellidae and the Arachnidiidae. Such a separation has been doubted by some earlier authors. A close examination of anatomical details reveals the general differences between victorelloid appendages and arachnidioid appendages. In victorellids the

appendages originate at distinct and more or less limited sites on the cystids, whether or not the potential appendages actually develop, and the appendages are never produced on the narrow and most proximal cystid part. In the Arachnidoidea, however, appendages may be formed irregularly at various sites of the cystid borders, including the narrow proximal cystid part. Appendages of different zooids may (but not necessarily) fuse histologically and often produce a new zooid at those points of fusion in arachnidioid species. This histological fusion does not occur in the victorelloid (and some stolonate) species (see Fig. 11).

In addition to observations of collected specimens, studies on living colonies of *Cryptoarachnidium argilla* have revealed the absolutely different growth potential of the arachnidioid cystid appendages. Banta (1967) originally described this species as *Victorella argilla*. Re-examination of paratype specimens showed that this species is undoubtedly not a victorelloid but an arachnidioid species, and the new genus *Cryptoarachnidium* was established (Jebram, 1973b). Specimens from Marina del Rey (California, U. S. A.) have been cultivated since October of 1977 in Braunschweig.

Cystid appendages apparently have developed independently in various phylogenetic lines in the Ctenostomata. Appendages are typical for most species of the Arachnidoidea but are formed also in several species of the Walkerioidea, e.g., *Aeverrillia setigera* (Hincks), and the Vesicularioidea, e.g., species of *Bowerbankia*, *Buskia*, and *Cryptopolyzoon*. This study has revealed that cystid appendages are common also in the Victorelloidea. In the latter superfamily, cystid appendages simply have been overlooked in some of the species in the past. The important characteristic for the placement of a species in a ctenostome superfamily, then, is not the presence or absence of cystid appendages but the details of their arrangement and growth potential.

Cultivation experiments as a taxonomic technique

Rogick agreed with Soule (1957) that some of the Salton Sea specimens were *Nolella blakei*. The confusion of those workers resulted mainly from the fact that the available animals were already preserved and were sexually immature. Voluminous ecological surveys and monographs (e.g., Schütz, 1963; Carrada and Sacchi, 1964) are less valuable if they are based partially or mainly on incorrect identification of some of the predominant primary consumers (bryozoans) in brackish habitats.

In microbiology and botany, experimental work as an aid for identification of species has a long tradition. In zoology, however, cultivation techniques for taxonomic purposes have been used for relatively few taxa, e.g., protozoans, some polychaetes and platyhelminths, certain parasitic or pathogenic species, and, of course, for various genetics studies. Most taxonomists and most workers in faunistics and synecology traditionally study preserved specimens. Although Braem (1951) demonstrated the usefulness of living animals for some more delicate taxonomic problems, this approach has been virtually neglected in other earlier bryozoan studies. The results described above reveal that the taxonomy in the Victorellidae, including reports from Asia and Africa, can be sufficiently determined only on the basis of living animals and with parallel-culture methods under defined conditions. There should be no doubt that taxonomy in various groups of the Bryozoa (and other taxa) requires experimental work and detailed studies on living animals. In some cases, future taxonomic investigation must include not only morphological features already present but also the growth *potential* of the zooids.

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